Diel Patterns of Vertical Distribution in Euthecosomatous Pteropods of Hawaiian Waters

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Abstract. Nineteen species of euthecosomatous pteropods were identified from epipelagic waters off Hawaii. Diel patterns of vertical distribution, abundance, and shell size were assessed from 32 tows taken through five depth intervals to 300 m during day and night periods using opening-closing 70 cm Bongo nets. Six species (*Limacina trochiformis*, *Creseis* sp., *C. virgula conica*, *Diacria danae*, *Diacavolinia angulosa*, and *Diacria costata*) were epipelagic and showed limited to no diel differences. Thirteen species (*L. inflata*, *Styliola subula*, *L. bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa*, *L. lesueuri*, *C. inflexa*, *Cuvierina columnella*, *Hyalocylis striata*, *Diacria maculata*, *Cavolinia gibbosa*, and *Diacria major*) were either epipelagic/mesopelagic or mesopelagic, and showed an increase in total mean abundance at night. Diel differences in vertical distribution are most parsimoniously interpreted as upward nocturnal migrations. The results of this study are in general agreement with those obtained for the same species in the North Atlantic Ocean and Caribbean Sea.

INTRODUCTION

The euthecosomatous (or shelled) pteropods are widely distributed in the world's oceans and the majority of species dwell in the epipelagic zone, although a few are mesopelagic or bathypelagic (Bé and Gilmer, 1977). Our understanding of their vertical distribution patterns is based mainly on studies that have employed stratified-oblique or discrete-depth tows carried out in the North Atlantic Ocean (Wormelle, 1962; Myers, 1967; Haagensen, 1976; Wormuth, 1981; and Andersen et al., 1997). The most comprehensive of these studies (Wormuth, 1981) employed stratified tows taken through discrete depth intervals to 1000 m during day and night periods. *Limacina inflata* (d'Orbigny, 1836), *L. lesueuri* (d'Orbigny, 1836), *Styliola subula* (Quoy and Gaimard, 1827), and *Clio pyramidata* Linnaeus, 1767 were characterized as strong migrators, with peak abundances at depths of 200–400 m during the day and <100 m at night. *Limacina trochiformis* (d'Orbigny, 1836), *L. bulimoides* (d'Orbigny, 1836), *Clio cuspidata* (Bosc, 1802), *Creseis acicula* (Rang, 1828), and *C. virgula* (Rang, 1828) showed highest daytime and nighttime abundances at depths <100 m (i.e., they were shallow-water non-migrators).

Vertical distribution data in the Pacific Ocean come from only two studies. The first was conducted by McGowan (1960) in the North Pacific and sampled the upper 140 m during day and night periods by oblique tows with continuously open and opening-closing nets. *Creseis virgula clava* (Tesch, 1948), *Clio pyramidata*, *Limacina inflata*, and *L. helicina* (Phipps, 1774) were captured in greater numbers at night than during the day, suggesting upward nocturnal migrations, while *Limacina trochiformis* and *Cavolinia longirostris* (de Blainville, 1821) were collected in comparable numbers during the day and at night. Twenty other species were identified, but no vertical distribution data were given. In the second study (Tanaka, 1970), vertical distribution records for individual species were not given except for *Limacina inflata*, which had maximal numbers at 50 m at night (but ranged downward to 550 m) and had an even distribution between the surface and 400 m during the day.

The present study on the diel vertical distribution and abundance of euthecosomes is the first from the Pacific Ocean based on replicated, opening-closing net samples. Oblique tows were taken through five depth intervals in the upper 300 m of the water column during day and night periods, and vertical patterns of distribution, density, and shell size are characterized for 19 species.

MATERIALS AND METHODS

The plankton samples used here come from a previous study designed to determine diel patterns of vertical distribution and abundance of squid paralarvae (Young and Harman, 1985 and Harman and Young, 1985) and heteropod gastropods (Seapy, 1990). Plankton tows were taken in waters southwest of the

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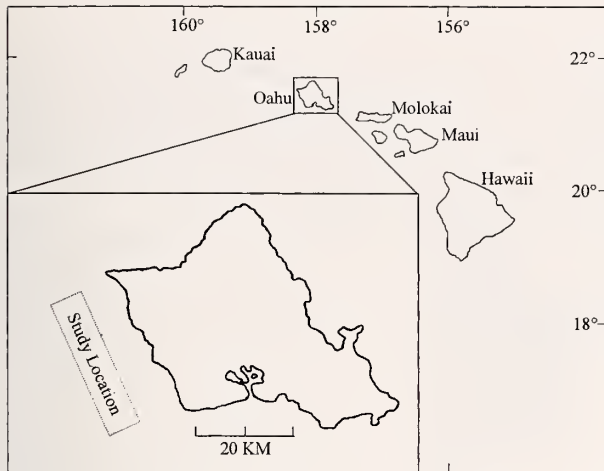
Figure 1. Hawaiian Archipelago and the location of the sampling area off the southwest side of the island of Oahu.
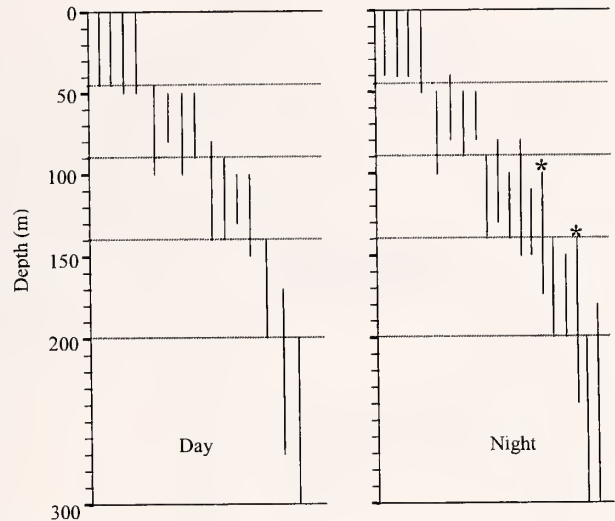

Figure 2. Depth ranges of tows taken during day and night periods. Vertical lines represent depth ranges of individual tows. Horizontal dotted lines indicate the adjusted depths of each sample depth interval. Asterisks mark the two tows that were not used in the analysis.

Hawaiian island of Oahu (Figure 1) aboard the R/V *KANA KEOKI* of the University of Hawaii between 9 and 15 April 1984. The study area was located in waters that averaged 2000 m in depth and ranged from 11 to 20 km off shore (Figure 1). Samples were collected with opening-closing, 70-cm diameter (0.385 m²) Bongo nets constructed of 0.5 mm Nytex cloth. The nets were fished obliquely through six target depth intervals (0–50, 50–100, 100–150, 150–200, 200–300 and 300–400 m) comprising the epipelagic zone off Hawaii (Young et al., 1980) for thirty minutes in each depth stratum during day and night periods (Figure 2). Unfortunately, difficulties encountered in completing tows in the 300–400 m interval resulted in only one successful tow during the day between 280 and 380 m (Seapy, 1990). Because there was no replication and no nighttime samples, the 300–400 m interval was omitted from the present study.

Previous research (Snider, 1975; cited in Wormuth, 1986) has shown that collection of larvae and young post-metamorphic individuals of *Limacina inflata* and *L. trochiformis* was greatly increased by using nets with a mesh size of 0.183 mm instead of 0.505 mm. Shell diameter at metamorphosis of *L. inflata* and *L. retroversa* (Flemming, 1823) is about 0.4 mm (discussed in Lalli and Gilmer, 1989). Since this study does not include larvae, those post-metamorphic individuals of limacinids between 0.4 and 0.5 mm were undoubtedly undersampled. Based on Snider's (1975) size-frequency plots (reproduced in Wormuth, 1986), a 0.505 mm net collects about half as many individuals in the size range of 0.4–0.5 mm as a 0.183 mm net.

A Benthos Time-Depth Recorder was attached to the Bongo net frame, and the starting and finishing depths for each depth stratum were determined subsequent to the tows from resultant time-depth plots.
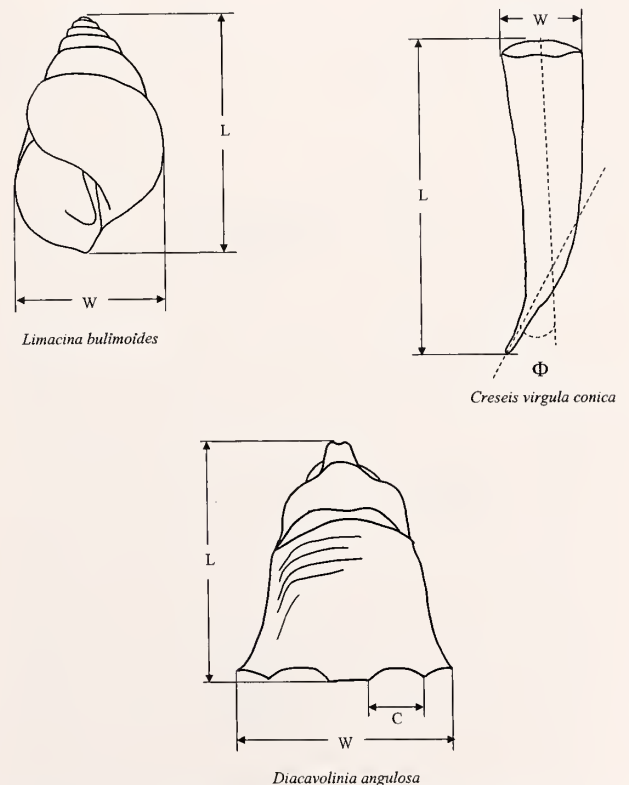

Figure 3. Euthecosome shell morphometrics. Where: L = length, W = width, Φ = posterior angle, and C = caudal fold width.

Table 1

Water column densities (numbers of individuals beneath 100 m^2 of ocean surface) for day and night periods and assignment of species to vertical groupings. To facilitate comparisons between species, the nighttime densities are also expressed as percentages. Differences in water column densities between day and night periods were assessed using a χ^2 test (where: s = significant at $P = \leq 0.05$ and ns = not significant). Each species was placed into either an epipelagic (=1) or epipelagic/mesopelagic and mesopelagic (=2) group (see results). Vertical groups shown in parentheses are hypothesized due to lack of statistical support.

| | Density | | | | Vertical group |
Species	Night	Percentage	Day	Significance	
Limacina inflata	1514.9	34.5	93.2	s	2
Styliola subula	734.6	16.7	56.0	s	2
Limacina trochiformis	733.6	16.7	1014.4	s	1
Limacina bulimoides	409.2	9.3	209.1	s	2
Creseis acicula	233.6	5.3	57.7	s	2
Clio pyramidata	201.8	4.6	14.8	s	2
Cavolinia globulosa	180.4	4.1	142.5	s	2
Limacina lesueuri	153.4	3.5	3.9	s	2
Creseis sp.	63.3	1.4	57.5	ns	1
Cavolinia inflexa	46.6	1.1	23.0	s	2
Creseis virgula conica	45.1	1.0	57.6	ns	1
Diacria danae	18.9	0.4	21.5	ns	1
Cuvierina columnella	17.9	0.4	0.0		(2)
Diacavolinia angulosa	10.9	0.3	17.4	ns	1
Diacria costata	10.0	0.2	7.9	ns	1
Hyalocylis striata	7.7	0.2	0.0		(2)
Diacria maculata	3.5	0.1	0.0		(2)
Cavolinia gibbosa	2.0	0.1	0.0		(2)
Diacria major	0.5	<0.1	0.0		(2)
Total	4387.9		1776.5		

The dates and times of the tows used here are given in Nigro (2002). Recorded ranges for the depth strata were reasonably accurate in the 0–50 and 50–100 m targeted intervals, but progressively less so for the deeper intervals (Figure 2). The cause of the inaccuracies at increased depth was that prior to each tow, we had to estimate the length of wire paid based on the wire angle (determined using a hand-held wire angle indicator) and the maximal target depth (by division of the target depth (m) by the cosine of the wire angle). Because the cable is progressively less likely to remain straight as depth increases, achieving the target depths by this method become progressively less accurate.

Based on the recorded depth ranges of the tows, five sample depth intervals were established: 0–45, 45–90, 90–140, 140–200, and 200–300 m (Figure 2). These depth intervals were chosen to minimize the amount of overlap between adjacent intervals, as most tows ranged somewhat outside their targeted depth interval. Tows that ranged outside a depth interval but that fished mostly within it were considered to have fished entirely within that interval. Also, tows that ranged through only part of a depth interval but did not extend into another one were considered to have fished entirely within it. We made one exception to this requirement; the first of two daytime tows in the 200–300 m sample

depth interval was assigned to that interval, even though it ranged 30 m into the 140–200 m interval.

Two plankton samples (port and starboard) were collected during most tows. During five tows, however, the port or starboard net became fouled and only the sample from the open net was available. Also, either the port or starboard sample was not used from four tows because of poor sample preservation. Altogether, 55 plankton samples from the 32 tows were used in the analysis. At least four replicate samples each for the day and night periods were used from the first three depth intervals (0–45, 45–90, and 90–140 m). One and two samples for the day and night periods, respectively, were used for the 140–200 m depth interval. For the 200–300 m depth interval, two samples were used for each diel period.

The volume of water filtered during each tow was calculated based on the number of revolutions recorded by calibrated T.S.K. Model OI-210 Flow Meters mounted inside the frame of each net. The volume of water filtered during each tow averaged of 2841 m^3 and ranged from 1142 to 6027 m^3 (Nigro, 2002). Expendable Bathythermograph (XBT) casts were made daily during the cruise. There was little variability between the results from day to day. Briefly, the average surface temperature was about 25°C and the mixed layer
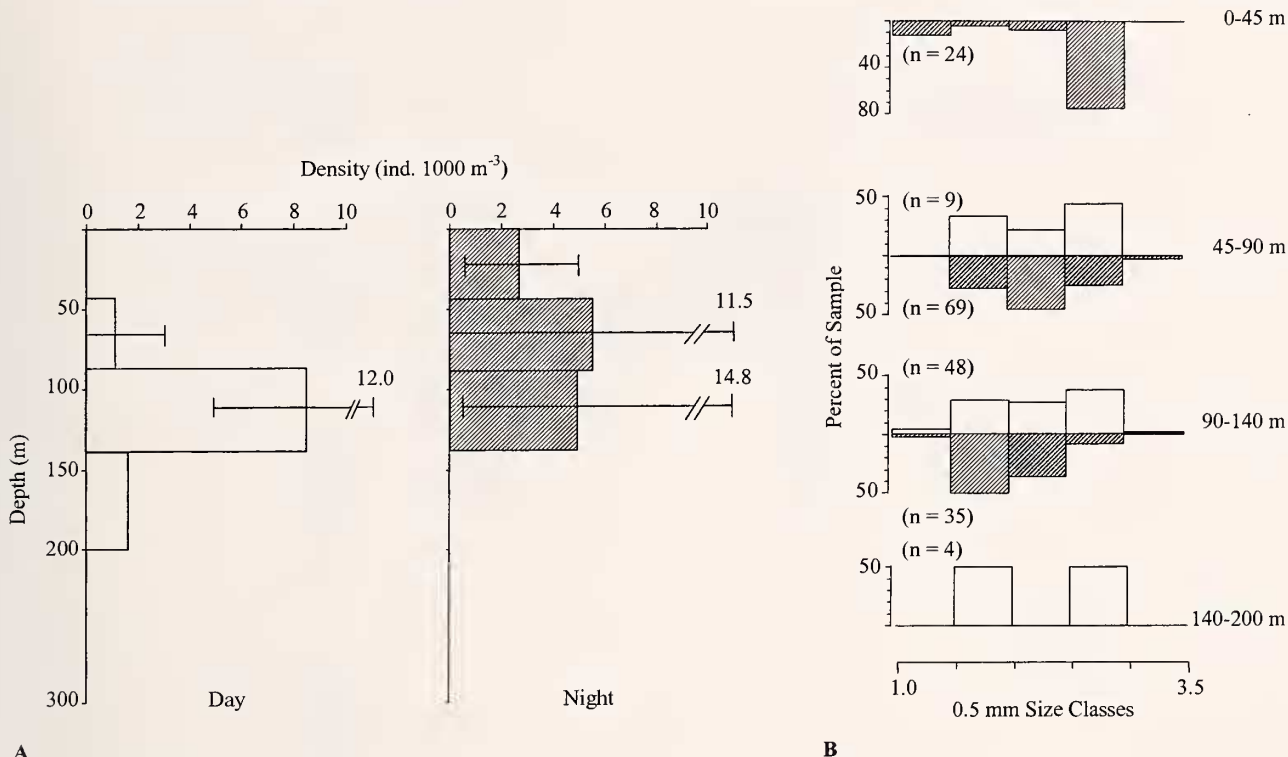
Figure 4. *Creseis* sp. (A) Mean densities (ind. 1000 m⁻³) in each depth interval during day (open bars) and night (hatched bars) periods. At the midpoint of each depth interval, ranges of densities among replicated tows are indicated by horizontal bars. (B) Percent of individuals in each size class from each depth interval during the day (open bars above the x-axis) and night (hatched bars below the x-axis). The number of specimens measured is indicated in parentheses.
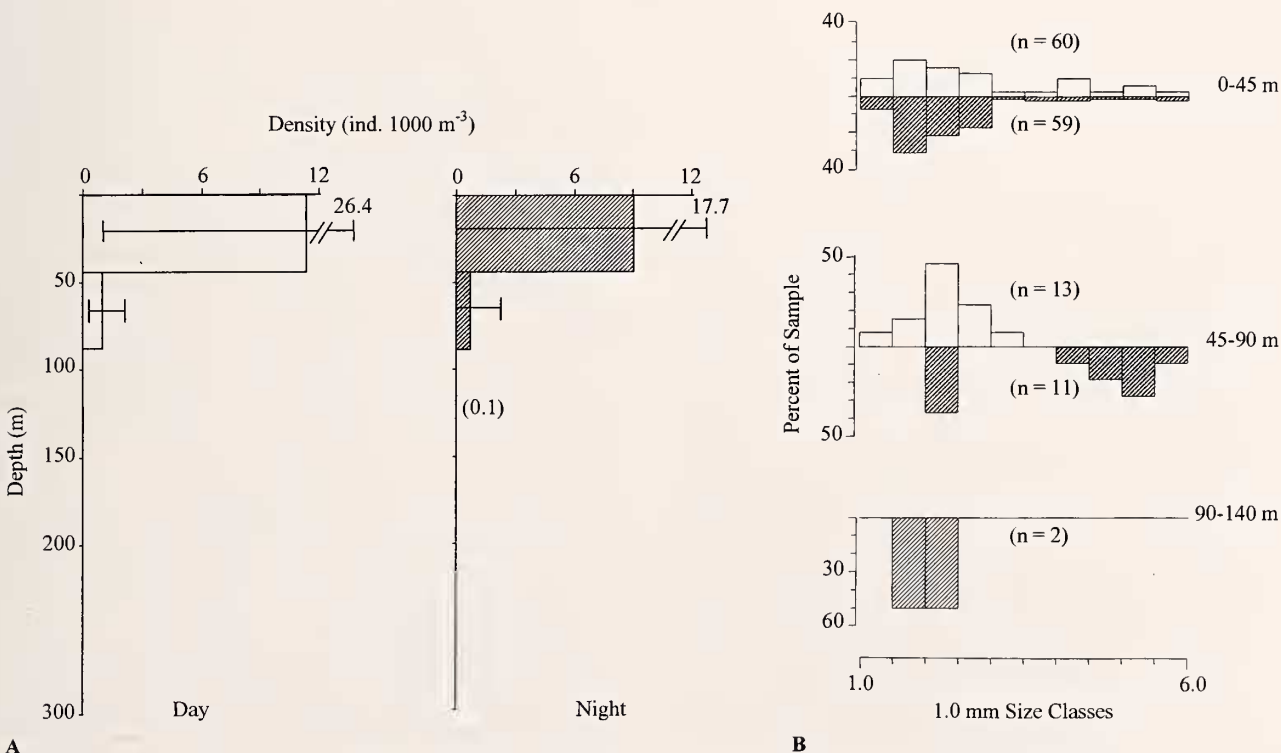

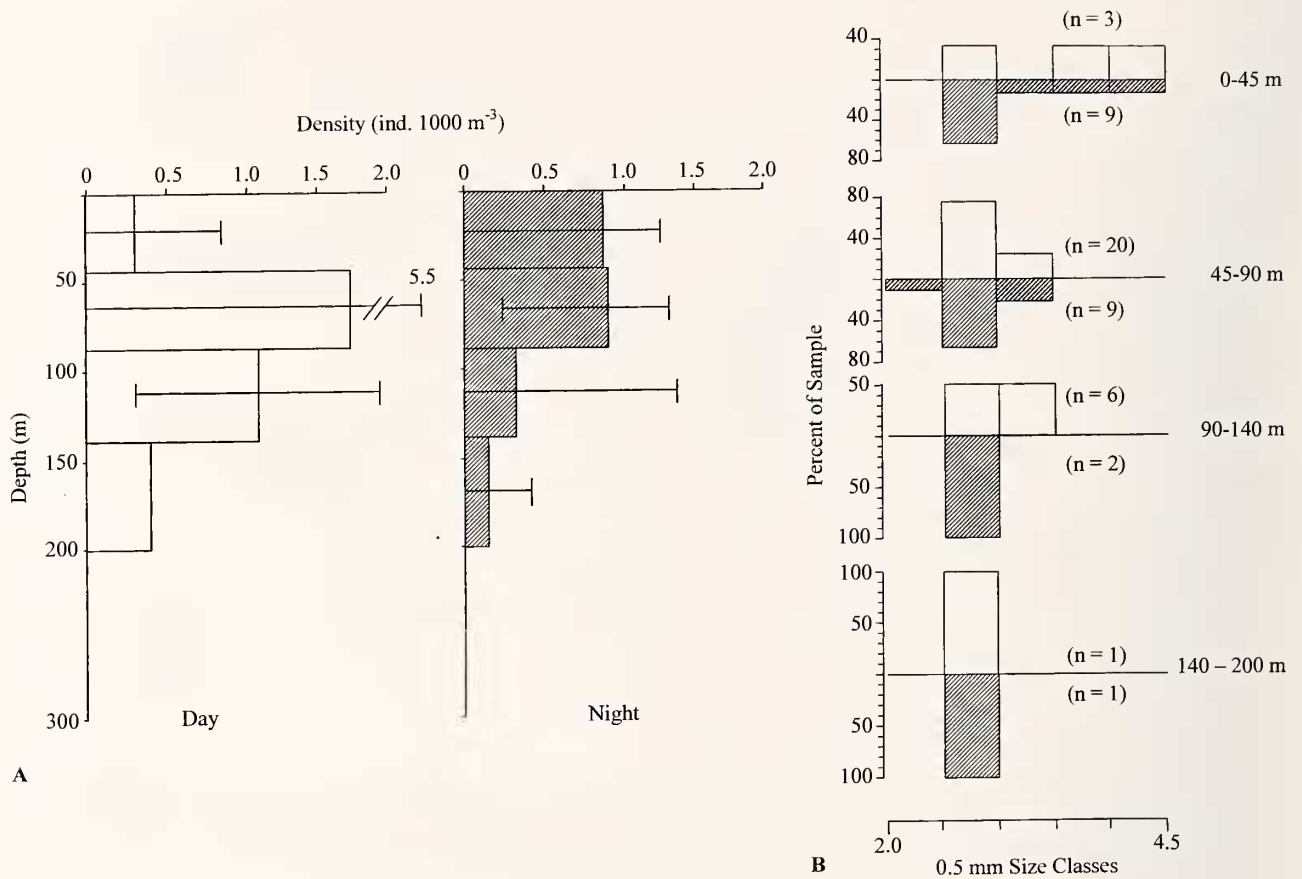Figure 5. *Creseis virgula conica.* Legend as for Figure 4.

Figure 6. *Diacavolinia angulosa.* Legend as for Figure 4.

extended to about 65 m, below which the temperature decreased steadily to about 10°C at about 300 m and about 6°C at 500 m.

Plankton samples were fixed in 4% buffered seawater-formalin for 48 hr, after which they were transferred to 40% isopropanol. All euthecosomes were removed from the samples. Species identifications were based primarily on Bé and Gilmer (1977), van der Spoel (1967), and van der Spoel et al. (1997); for details see Nigro (2002). One species of *Creseis* was not described in the literature and is referred to here as *Creseis* sp.

Each species was enumerated using a Wild M5A stereomicroscope and the counts were converted to density values expressed as individuals per 1000 m³ (ind. 1000 m⁻³). The species densities of the port and starboard nets for each tow were calculated separately and then averaged. Day and night density data were compared by means of Poisson regression analysis using the SAS version 8.01 statistical package. For each species an interaction effect was assessed between depth and diel period. For each species with a significant interaction, differences between day and night densities were compared within each depth interval.

Shell sizes were determined using the aforementioned stereomicroscope fitted with a calibrated ocular micrometer. In a given sample, all individuals belonging to a species were measured if the number was less than 100. For those species that occurred in numbers greater than 100 per sample, at least 100 randomly selected individuals were measured (see Nigro, 2002).

Shell diameters were measured for most species in the Family Limacinidae, as the shells in this family are coiled and increase in diameter with growth. Diameters were measured from the outside margin of the aperture to outside of the last whorl with the shell apex in an upward direction. For *Limacina bulimoides*, however, shell length was used instead of diameter because length is greater than diameter in this species (Figure 3) and, thus, is a better indicator of shell size. For species in the Family Cavoliniidae, shell lengths were measured from the posterior to the anterior margins of the shells (Figure 3). For identification purposes, the posterior angle for some *Creseis* spp. and caudal fold width for *Diacavolinia* sp. was measured (Figure 3).

Size-frequency distributions were constructed within each depth interval for each species. Mean sizes were compared between day and night periods within each depth interval by one-way ANOVA using Minitab
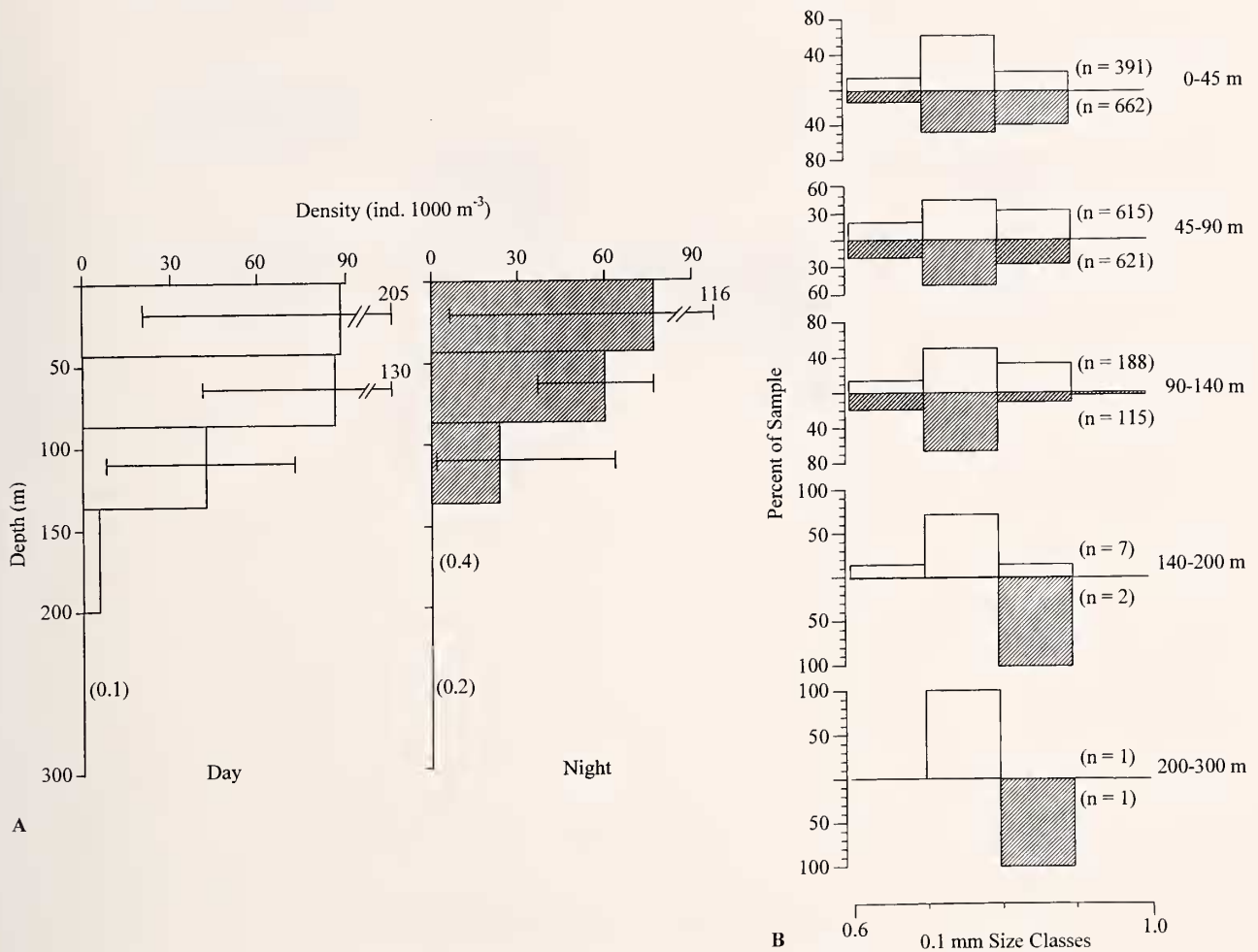
Figure 7.   *Limacina trochiformis*. Legend as for Figure 4.

version 9.0. Tukey's option was used to correct the error rate since multiple comparisons of means were made.

After completion of the present study, the sample residues were transferred to the Marine Biodiversity Processing Center of the Los Angeles County Museum of Natural History where they are housed under "Hawaiian Bongo Net Collection" (<http://collections.nhm.org/collection.html?code=bongo>).

RESULTS

Water column densities (number of individuals beneath 100 m² of ocean surface) were computed for each species during day and night periods (Table 1). The combined nighttime density for all species (4388 ind. 100 m⁻²) was nearly two and one-half times greater than the total daytime density (1777 ind. 100 m⁻²). Three species (*Limacina inflata*, *Styliola subula*, and *L. trochiformis*) had densities of 1515 to 734 ind. 100 m⁻²,

and together represented 68% of the total nighttime density. Eight species (*Limacina bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa* (Gray, 1850), *Limacina lesueuri*, *Creseis* sp., *Cavolinia inflexa* (Lesueur, 1813), and *Creseis virgula* (Rang, 1828) *conica* Eschscholtz, 1829) had nighttime densities between 409 and 45 ind. 100 m⁻², comprising 30% of the total. The last eight species had nighttime densities of less than 19 ind. 100 m⁻², making up the remaining 2% of the total.

The water column densities during day and night periods were compared by χ^2 analysis (Table 1). Nine of the eleven species with the highest total mean nighttime densities (>45 ind. 100 m⁻²) showed significant diel differences. Only one of those that were significantly different, *Limacina trochiformis*, was more abundant during the day. A total of five species showed no significant diel differences, and five species were collected only at night.

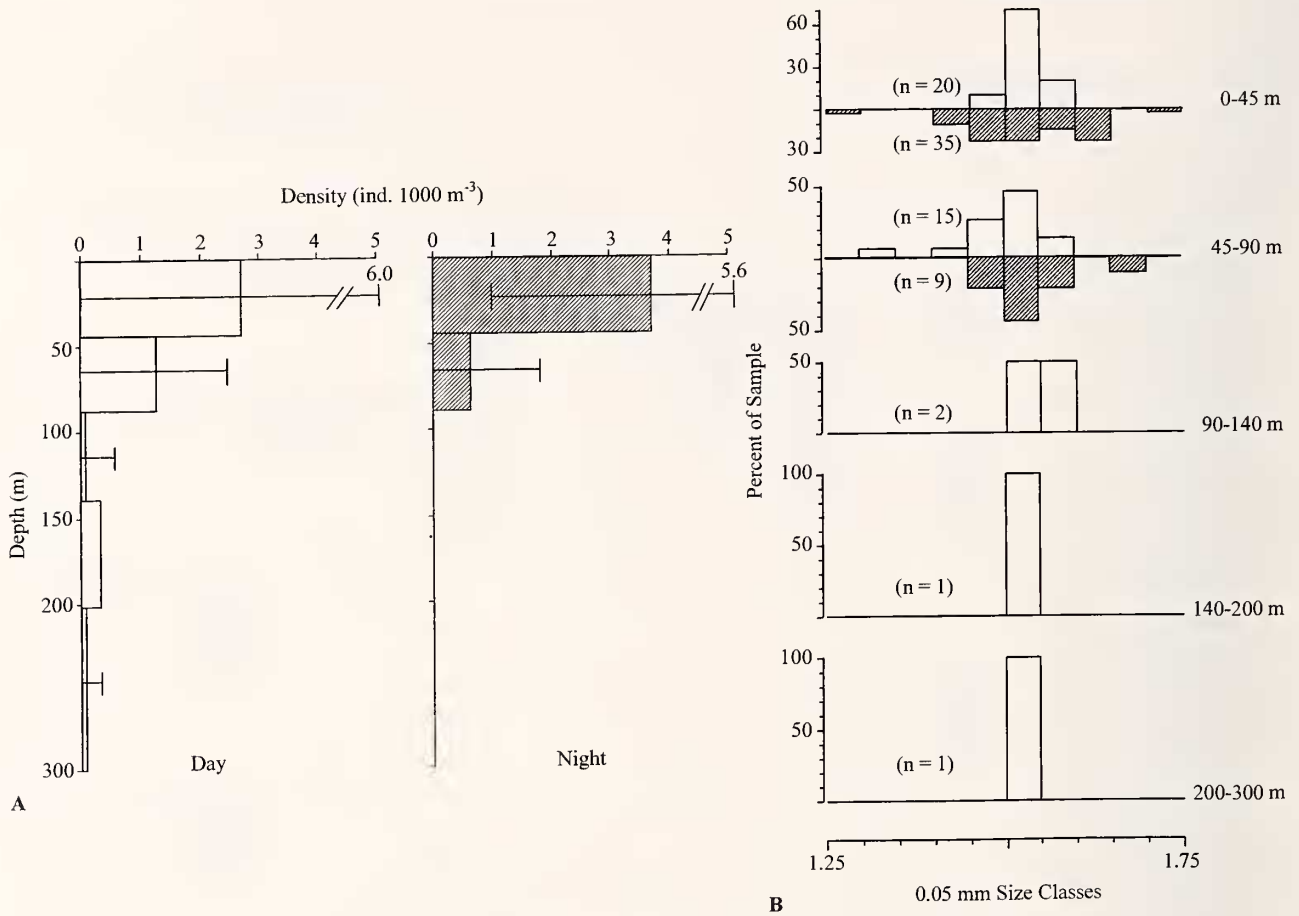Based on the above results, each species was placed

Figure 8. *Diacria danae*. Legend as for Figure 4.

into one of two vertical daytime groupings (Table 1, last column). The first group (epipelagic) was composed of those species present in comparable densities during both day and night periods with the exception of one, *Limacina trochiformis*, which was captured in significantly greater numbers during the day. The second group (epipelagic/mesopelagic and mesopelagic) is inferred from the results and, therefore, is hypothetical because samples were not collected from the mesopelagic zone. This group consisted of species that were either present in the epipelagic zone in significantly higher numbers during the night or were absent from the daytime samples. Individual depth interval means and tests for significance for each species in the two groups are summarized in Nigro (2002).

Epipelagic Species Group

Three species (*Creseis* sp., *C. virgula conica*, and *Diacavolinia angulosa* (Eydoux and Souleyet, Ms.)(Gray, 1850)) had water column densities that were comparable between day and night (Table 1) and

were restricted to the upper 200 m. For *Creseis* sp., all but four specimens (in the daytime 140–200 m samples) were collected in the upper 140 m (Figure 4A). Individuals in the 0–45 m interval were found only at night, and a significantly greater mean nighttime density was found in the 45–90 m interval. The sum of the mean densities below 90 m was about twice as great during the day than at night, but the difference was not significant. Shell lengths ranged from 1.0 to 3.5 mm (Figure 4B), and no significant differences were found between diel periods.

Creseis virgula conica was limited to the upper 90 m during the day and night (Figure 5A), except for two individuals captured in the nighttime 90–140 m samples. Replicate variability was high above 90 m during both diel periods. Higher daytime densities were recorded from both the 0–45 and 45–90 m depth intervals, but the differences were not significant. Shell lengths ranged from 1.0 to 6.0 mm (Figure 5B). Mean shell lengths were similar in the 0–45 interval, but were significantly greater at night than during the day in the 45–90 m interval.
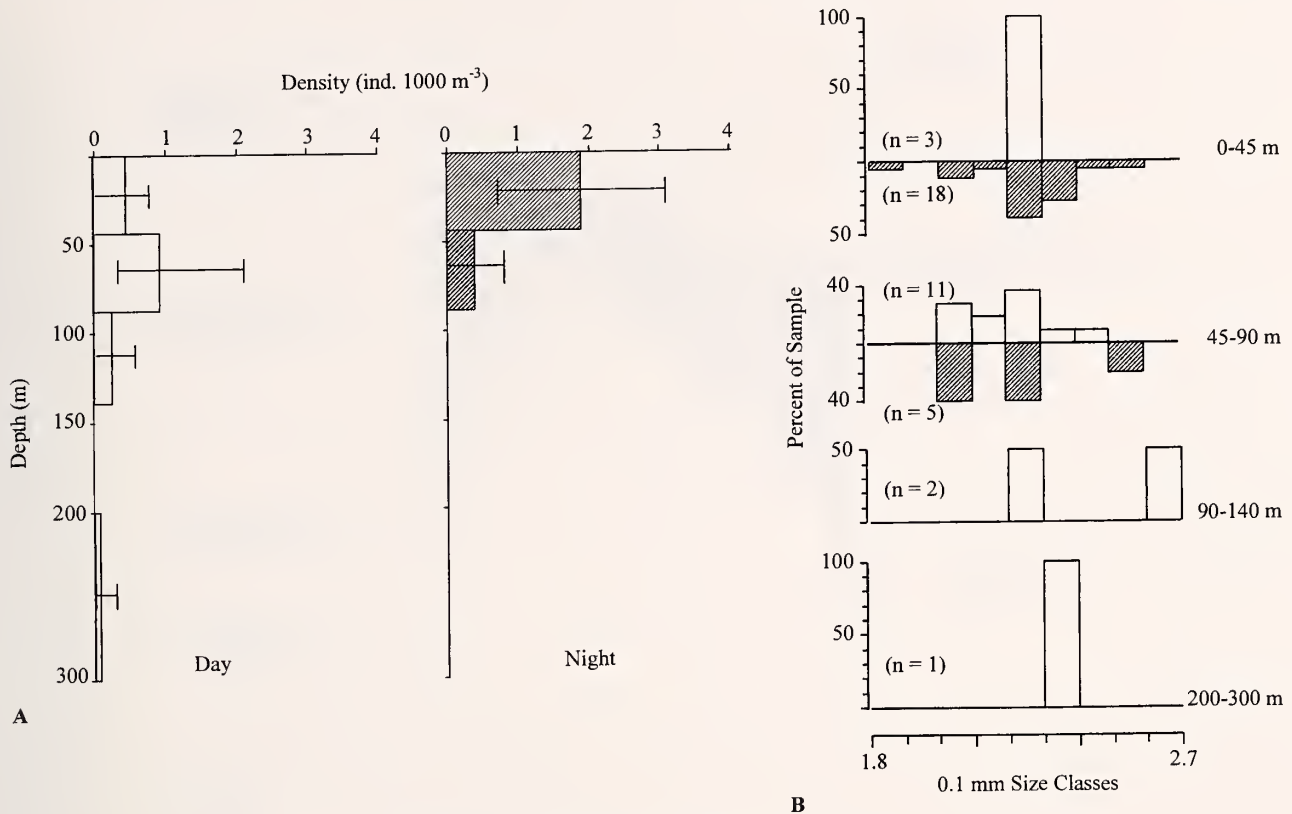
Figure 9. *Diacria costata*. Legend as for Figure 4.

Diacavolinia angulosa was recorded in waters above 200 m during both day and night periods (Figure 6A). Mean densities were low (<2 ind. 1000 m^{-3}) with high replicate variability and no significant differences between diel periods. Shell lengths ranged from 2.0 to 4.5 mm and did not differ significantly between day and night periods, although the largest individuals (>3.5 mm) were taken only from the upper 45 m (Figure 6B).

Three species (*Limacina trochiformis*, *Diacria dane* van der Spoel, 1968, and *D. costata* Pfeffer, 1879) had daytime water column densities that were similar to their nighttime densities except for *L. trochiformis*, which had greater densities during the day (Table 1), and extended to 300 m. *Limacina trochiformis* was most abundant above 90 m, with lower densities in the 45–90 m interval and low to very low densities extending down to 300 m (Figure 7A). Replicate variability was high with daytime densities higher in all depth intervals above 200 m, but the diel differences were not significant. Shell diameters ranged narrowly between 0.6 and 1.0 mm (Figure 7B). A significantly larger mean shell diameter was found at night in the 0–45 m interval, but the small (0.02 mm) difference was probably biologically meaningless.

Diacria danae was found from the surface to 300 m during the day and was limited to the upper 90 m at

night (Figure 8A). Maximal densities were found above 45 m during both day and night periods. Variability was high among replicates, with no significant differences in density between diel periods. Shells ranged narrowly between 1.25 and 1.75 mm (Figure 8B). The largest individuals (>1.60 mm) were found only in night samples, but diel differences were not significant.

Diacria costata ranged from the surface to 300 m during the day and was restricted to the upper 90 m at night (Figure 9A). During the day, the majority of individuals were found in the 45–90 m interval, and in the 0–45 m interval at night. Nighttime densities were significantly higher compared to the day in the 0–45 m depth interval. Although daytime densities in the 45–90 m interval were about three times higher than at night, the difference was not significant. Shell sizes ranged from 1.8 to 2.7 mm (Figure 9B) and were comparable between diel periods in the 0–45 and 45–90 m depth intervals.

Epipelagic/mesopelagic and Mesopelagic Species Group

Eight species (*Limacina inflata*, *Styliola subula*, *L. bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa*, *L. lesueuri*, and *Cavolinia inflexa*) had
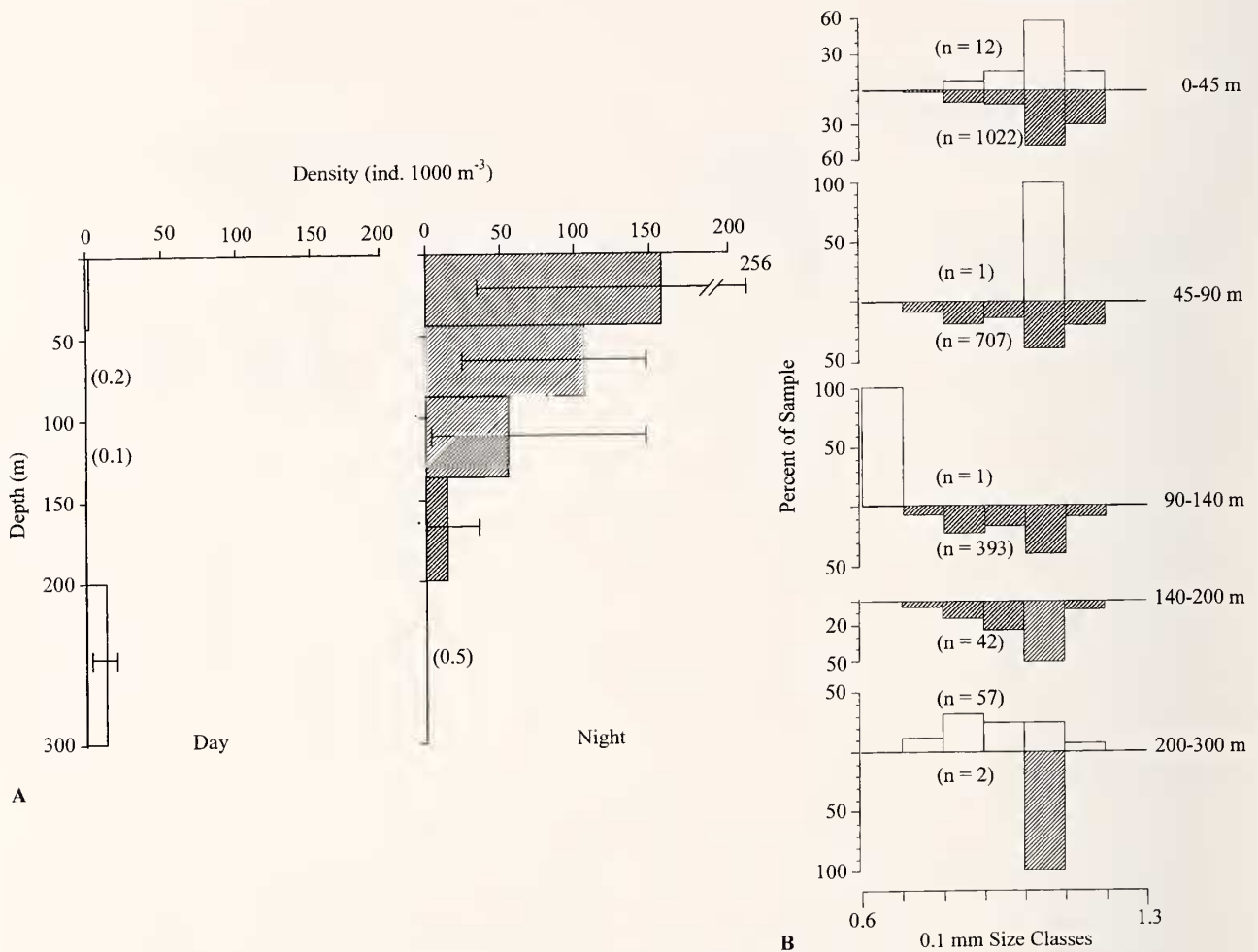
Figure 10.   *Limacina inflata*. Legend as for Figure 4.

daytime water column densities that were significantly lower than nighttime densities in the upper 300 m (Table 1). These species are hypothesized to be daytime occupants of the epipelagic/mesopelagic and mesopelagic zones.

Limacina inflata was captured from surface waters to 300 m during both diel periods (Figure 10A), except that it was absent from 140–200 m during the day. At depths above 200 m it was recorded in very low numbers during the day. At night replicate variability was high, and significantly greater numbers were captured above 140 m with a maximum in the 0–45 m depth interval. No significant diel differences were found below 140 m, although the mean daytime density in the 200–300 m interval was 17 times greater than at night. Shell diameters ranged from 0.6 to 1.3 mm, and were not significantly different in the 0–45 m interval (Figure 10B). Small sample sizes (n ≤ 2) in deeper intervals from either day or night periods prohibited statistical comparisons.

Styliola subula was present in low to very low numbers above 200 m during the day, and it was restricted to the upper 200 m at night (Figure 11A). It exhibited high replicate variability at night and increased from low numbers at 140–200 m to a maximum in the upper 45 m. Significantly greater densities were found only at night in depth intervals above 140 m. The mean nighttime density at 140–200 m was higher than during the day, but the difference was not significant. Shell lengths ranged broadly from 1.0 to 9.0 mm. No significant differences in shell sizes (Figure 11B) were found, although individuals larger than 5.0 mm were taken only from night samples.

Limacina bulimoides was captured from surface waters to 300 m during the day with density increasing with depth, and it was mainly found in the upper 140 m at night (Figure 12A). Nighttime densities were significantly greater compared to the day in depths above 140 m. Replicate variability was high at night with
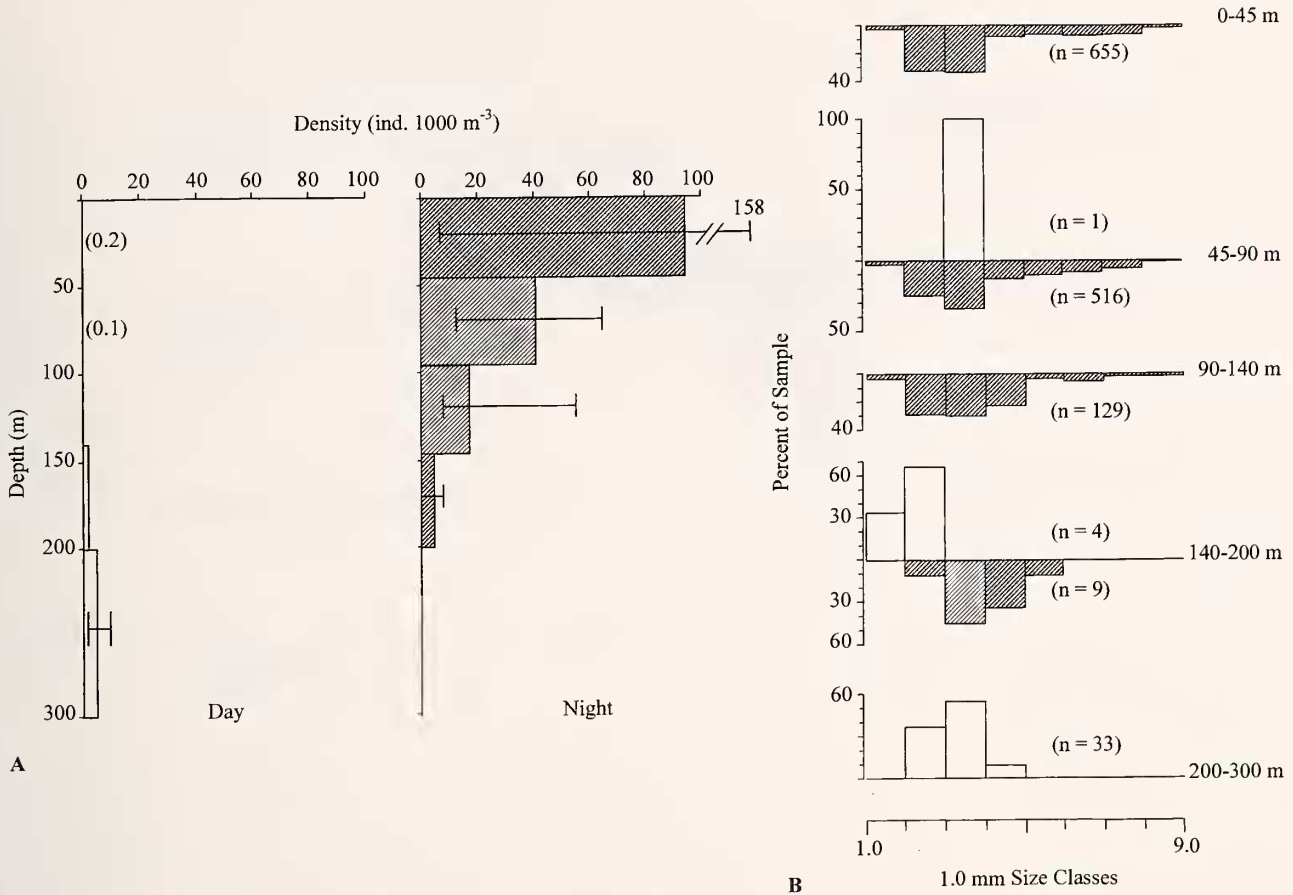
Figure 11. *Styliola subula*. Legend as for Figure 4.

densities increasing from a low at 140–200 m to a maximum at 0–45 m. The mean daytime density between 140 and 200 m was higher than at night, but the difference was not significant. Shell lengths ranged narrowly from 0.6 mm to 1.6 mm and were significantly larger at night in the 90–140 m depth interval (Figure 12B). In waters above 90 m, the largest individuals (>1.4 mm) were taken only at night.

Creseis acicula was present in low numbers from the surface to 300 m during the day and was restricted to waters above 200 m at night, although it was only abundant above 90 m (Figure 13A). High replicate variability was found among the night tows above 90 m. Nevertheless, nighttime densities were significantly greater than daytime densities in the 0–45 and 45–90 m intervals. Most (80%) of those individuals captured at night were in the 0–45 m interval. Shell lengths ranged broadly from 2.0 to 9.0 mm (Figure 13B) with no significant diel differences, except in the 45–90 m interval where the mean length was significantly larger at night.

Clio pyramidata was absent from waters above 140 m and was scarce (mean abundances < 1.0 ind.

1000 m^{-3}) between 140 and 300 m during the day (Figure 14A). At night, this species was present only above 200 m with a maximal density in the 90–140 m interval. The total mean nighttime density was 20 times greater than during the day. Shell sizes varied widely from 1.0 to 13.0 mm (Figure 14B). Only the smallest shells (1.0–2.0 mm) were recorded from day tows. Large shells (>7.0 mm) were all recorded from night tows in the upper 90 m.

Cavolinia globulosa was present down to 140 m during the day and to 300 m at night (Figure 15A). Mean nighttime densities were significantly greater than daytime densities in the 0–45 m interval and significantly less in the 45–90 m interval. No significant differences were found below 90 m. Shell lengths ranged broadly from 0.5 to 6.5 mm and were significantly greater at night in all depth intervals above 140 m (Figure 15B). Large individuals (>3.5 mm) were collected only at night from tows above 200 m, except for one shell (5.5 mm) collected during the day from the 90–140 m interval.

Limacina lesueuri was present in very low numbers (<0.3 ind. 1000 m^{-3}) between the surface and 300 m
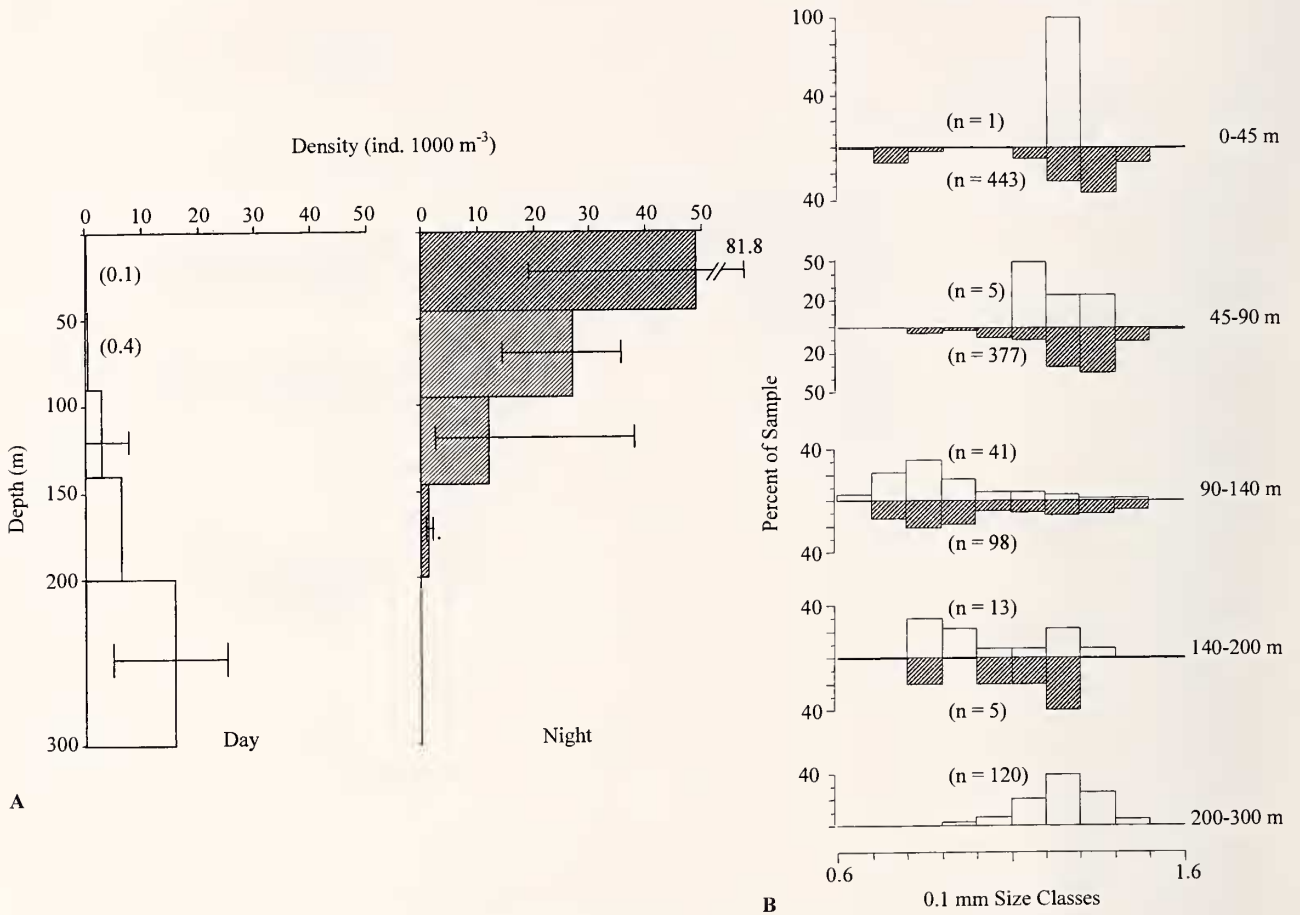
Density (ind. 1000 m^{-3})

Figure 12. *Limacina bulimoides*. Legend as for Figure 4.

during the day and was recorded in increasing numbers from 200 m to the 0–45 m interval at night (Figure 16A). Total mean nighttime densities were 52 times greater than daytime densities. Sixty-three percent of those captured at night were from the 0–45 m interval. Shell sizes ranged narrowly from 0.7 to 1.3 mm (Figure 16B) with the largest (>1.2 mm) captured only at night above 140 m. Many zero density samples prevented statistical comparison of density and size distributions.

Cavolinia inflexa was captured down to 300 m during the day and to 200 m at night (Figure 17A). Although slightly higher mean densities were recorded in all depth intervals at night, no significant differences were found, most probably due to the high replicate variability. Shells lengths ranged broadly from 1.0 to 6.0 mm. Those >2.5 mm were found only in the upper 140 m at night (Figure 17B), and individuals from the intervals above 90 m were significantly larger at night.

Five species (*Cuvierina columnella* (Rang, 1827), *Hyalocylis striata* (Rang, 1828), *Diacria maculata* Bleeker and van der Spoel, 1988, *Cavolinia gibbosa*

(d'Orbigny, 1836), and *D. major* (Boas, 1886)) were absent from the upper 300 m during the day (Table 1). These species are hypothesized to be daytime occupants of the mesopelagic zone. Except for *Cuvierina columnella* and *Hyalocylis striata*, which were captured in moderate to low numbers at night, the remaining three were captured in extremely low numbers at night and were not recorded from day tows. *C. columnella* was captured in the upper 200 m (Figure 18A), and most individuals (64%) were recorded from the 0–45 m interval. Shell lengths ranged narrowly between 7.0 and 8.0 mm (Figure 18B) with the largest individuals (>7.6 mm) between 45 and 90 m.

Hyalocylis striata was recorded only in waters above 90 m at night (Figure 19A). Mean densities were low (<1.0 ind. 1000 m^{-3}) and nearly the same in the 0–45 and 45–90 m intervals. Shell length ranged from 2.5 to 7.0 mm (Figure 19B) with shells larger than 3.5 mm taken only from the 45–90 m interval.

Diacria maculata and *D. major* were captured in extremely low numbers (five and one individuals, respectively) above 140 m at night. Sizes were not
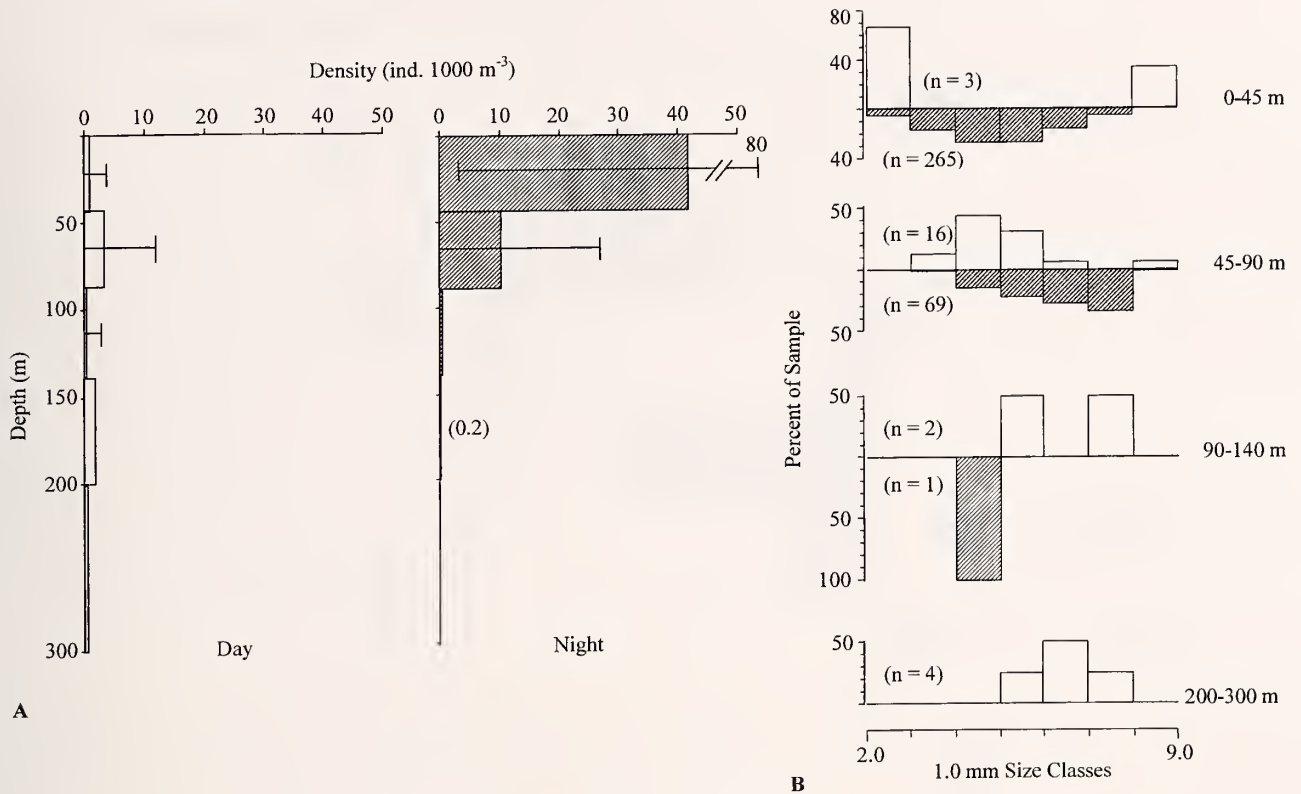
Figure 13. *Creseis acicula*. Legend as for Figure 4.

measured, as all shells were broken to some extent making size estimation unreliable. Lastly, a single *Cavolinia gibbosa* with a shell length of 9.2 mm was captured at night from the 200–300 m depth interval.

DISCUSSION

Based on the reviews of euthecosome taxonomy and biogeography by van der Spoel (1967), Bé and Gilmer (1977), and van der Spoel et al. (1997), and two subsequent taxonomic studies (van der Spoel and Pierrot-Bults, 1998 and Bontes and van der Spoel, 1998), 68 species of euthecosomes are currently recognized from the world's oceans. Half (34) have been reported from the tropical and/or subtropical Pacific Ocean (Table 2). McGowan (1960, 1963, 1971) identified 18 species with distributions that coincide with Hawaiian waters, all of which were collected in the present study with two exceptions. The first, *Cavolinia uncinata* (Rang, 1829), was classified as a tropical species by Bé and Gilmer (1977) and may be limited to lower latitudes south of the Hawaiian Islands. The second, *Cavolinia tridentata* (Neibuhr, 1775), was classified as subtropical and uncommon by Tesch (1948) and McGowan (1960).

Of the 19 species identified from the upper 300 m of the water column in the present study, 8 were present in significantly greater numbers at night than during the day while 5 were collected only at night, and, by implication, were below 300 m during the day. The most probable explanation for the difference in day-night densities for these 13 species is nocturnal vertical migration.

If a major adaptive value for nocturnal vertical migration is reduced visibility to visual predators during the day, then the shallowest daytime depths should coincide with that depth at which an individual ceases to present a perceptible visual cue (Angel, 1985). Off Hawaii, the shallowest daytime depth at which counterillumination can occur is 400 m, which coincides with the shallowest daytime depth of midwater micronekton (Young et al., 1980). This depth also should coincide with the shallowest daytime depth for mesopelagic euthecosomes and could explain the absence or low abundance during the day of the 13 species above 300 m in the present study. An alternate hypothesis explaining differences in density between day and night periods is the ability of animals to avoid an oncoming plankton net during the day.

Daytime net avoidance was hypothesized by McGowan and Fraundorf (1966) to be a function of net size. They found that 20- and 40-cm diameter nets (0.03 and 0.13 m²) underestimated euthecosome abundances obtained with a 140-cm net (1.54 m²). Nets with diameters
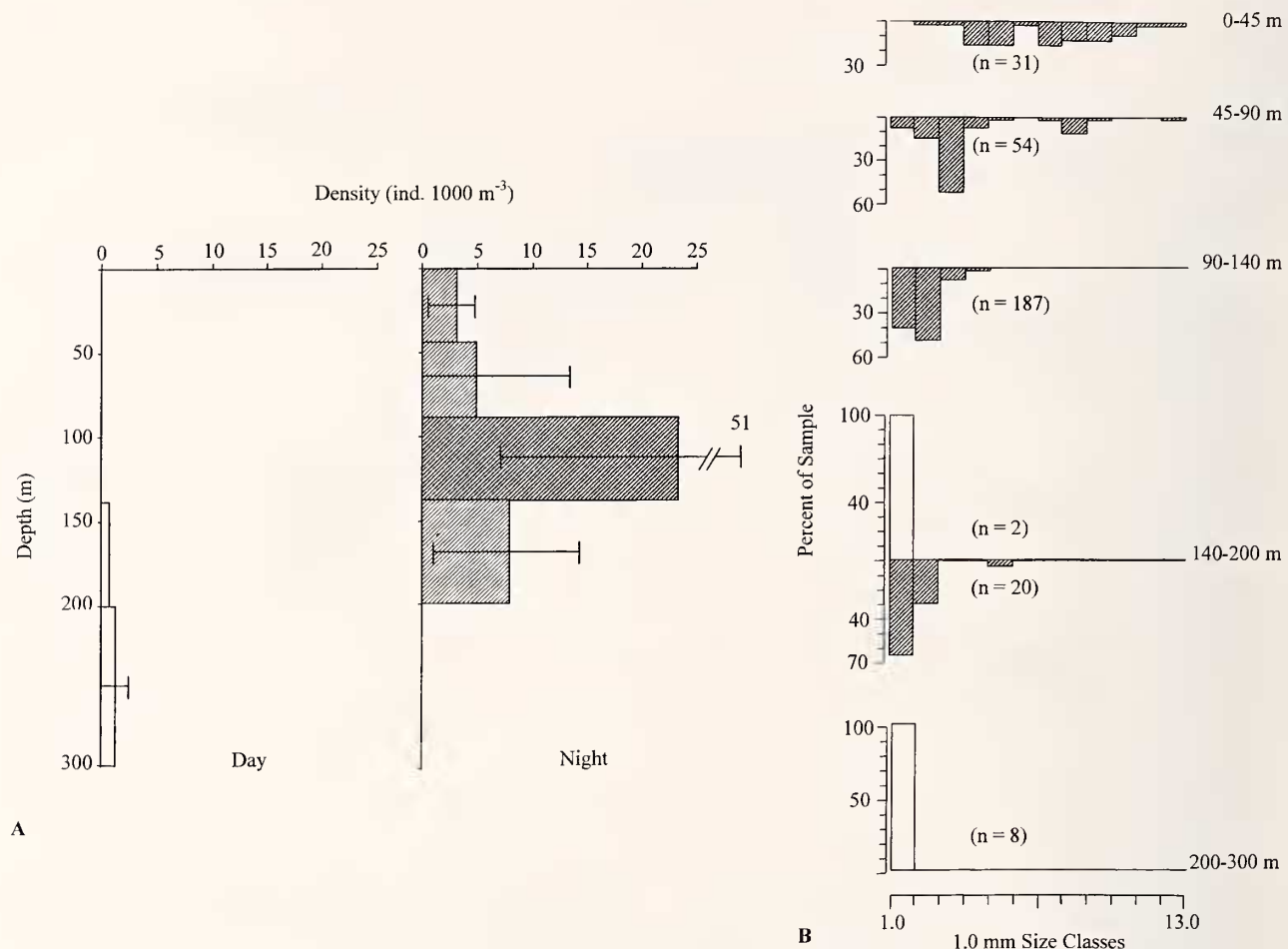
Figure 14. *Clio pyramidata.* Legend as for Figure 4.

of 60, 80 and 100 cm (0.28, 0.50, and 0.79 m²) gave intermediate results. Hypothetically, net avoidance of the 70-cm Bongo nets used here should be comparable with that obtained with their 60- and 80-cm nets. However, the paired 70-cm Bongo nets have unobstructed mouth openings while the individual nets used by McGowan and Fraundorf employed three-point towing bridles.

Strong support for an hypothesis that diel differences in density of euthecosomes at epipelagic depths are due to vertical migration and not net avoidance is given by data from Wormuth (1981). He compared the density of nine abundant euthecosomes from 22 day and night samples collected from nine discrete depth intervals to 1000 m using a 1-m² multiple open-closing net and environmental sensing system (MOCNESS). Like the Bongo nets, the mouth opening of the 1-m² nets was unobstructed. Wormuth found no significant difference between total species densities from day and night periods. Additional support for the above hypothesis is the lack of eyes or well-developed photoreceptors that

would be sufficiently sensitive to detect a change in light intensity produced by an oncoming net. Euthecosomes do possess one (in Limacinids) or two tentacles with tissue that may serve to detect differences in light intensity (Lalli and Gilmer, 1989). However, their ability to detect an oncoming net is improbable. A tactile function of the tentacles is probable, but such sensory receptors would operate equally as well during the day as at night to invoke net avoidance behavior.

For some species, it is also possible that larger individuals are more capable of daytime net avoidance than smaller ones. In the present study, we found that daytime tows in the upper 300 m collected only small individuals of *Cavolinia inflexa* (<2.5 mm) and *Clio pyramidata* (<2.0 mm), while nighttime tows collected individuals up to 6.0 mm and 13.0 mm, respectively. However, an alternate explanation is that resident daytime populations of small animals reside between the surface and 300 m, while larger individuals are found deeper.

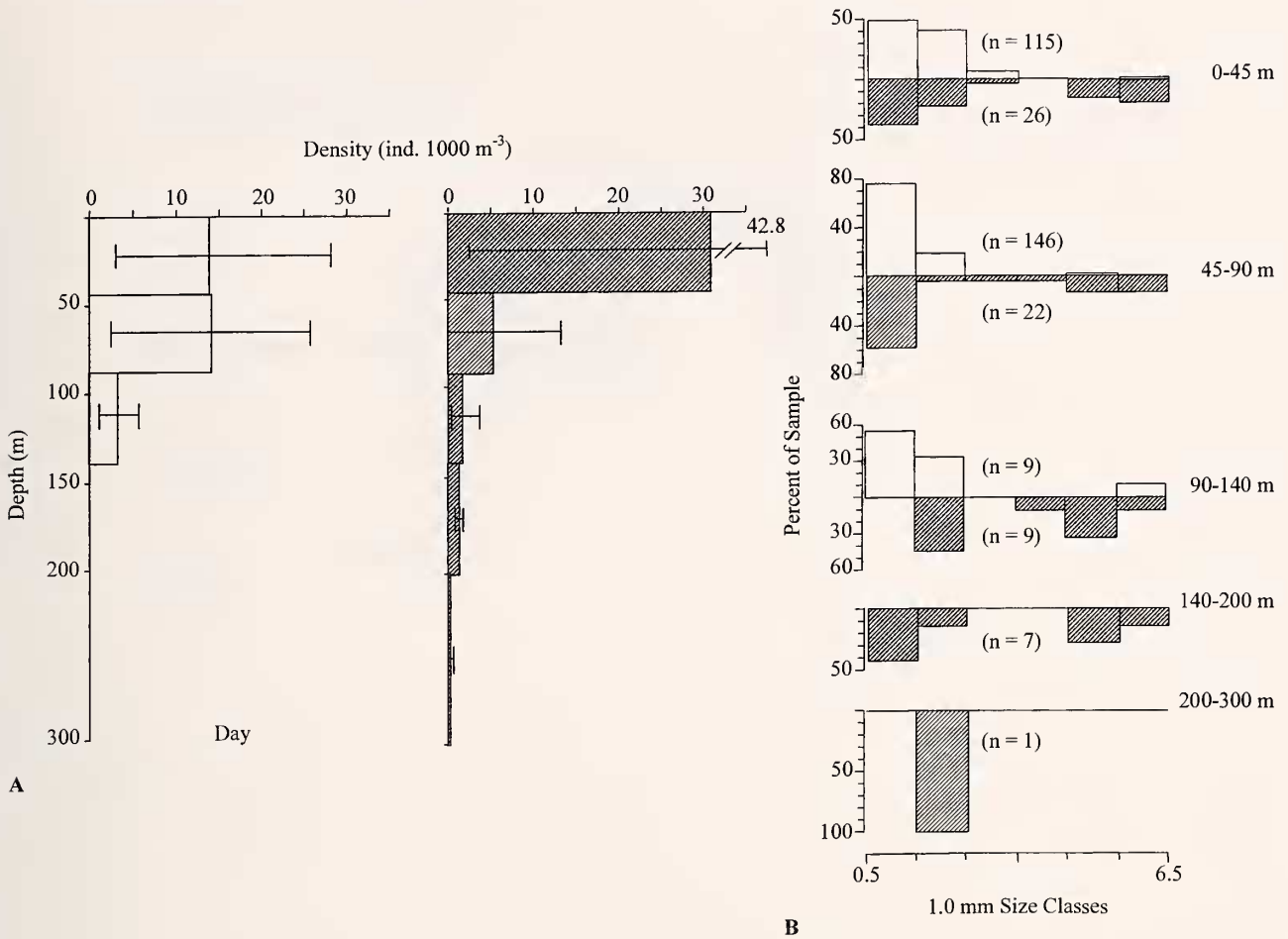Daytime and nighttime patterns of vertical distribu-

Figure 15. *Cavolinia globulosa*. Legend as for Figure 4.

tion would be expected to differ between localities mainly as a result of differences in light penetration, which is affected by water turbidity and season (at increasingly higher latitudes). Even in some tropical and subtropical areas, water clarity may vary due to seasonal upwelling and river runoff. In the eastern Caribbean, for example, massive freshwater runoff from the Orinoco River can cause dramatic changes in turbidity. This phenomenon has been observed on a seasonal basis far from the river mouth in the waters around Barbados (C. Lalli, personal communication). Secondary causes of variability in the depth of the epipelagic zone include increased turbulence due to storms, variations in light penetration due to atmospheric conditions, and variability in plankton density. For example, the samples used in the present study were collected during a period of seven days in the month of April with clear weather and calm seas. It is reasonable to expect that samples taken during other times of the year of the study may have yielded different results from those reported here. Lacking

information regarding the depth of the epipelagic zone at the localities and times of the previous studies in the North Atlantic (discussed below), the vertical distribution patterns characterized here from Hawaiian waters may or may not be directly comparable. Nonetheless, we decided that we should examine intra-species patterns reported by previous authors whose studies were conducted in the western North Atlantic with the aforementioned aspects serving as an explanatory framework for differences that may occur.

Among the six species classified as epipelagic in the present study, three (*Limacina trochiformis*, *Creseis virgula conica*, and *Diacavolinia angulosa*) showed no evidence of migration, while three (*Creseis* sp., *Diacria danae*, and *D. costata*) performed limited nocturnal migrations. Wormuth (1981) found that *L. trochiformis* and *C. virgula conica* from the Sargasso Sea were non-migrators with peak abundances above 100 m and 200 m, respectively, during both day and night periods. These results are similar to those of the present study, where >50% of the sampled population of *L.*
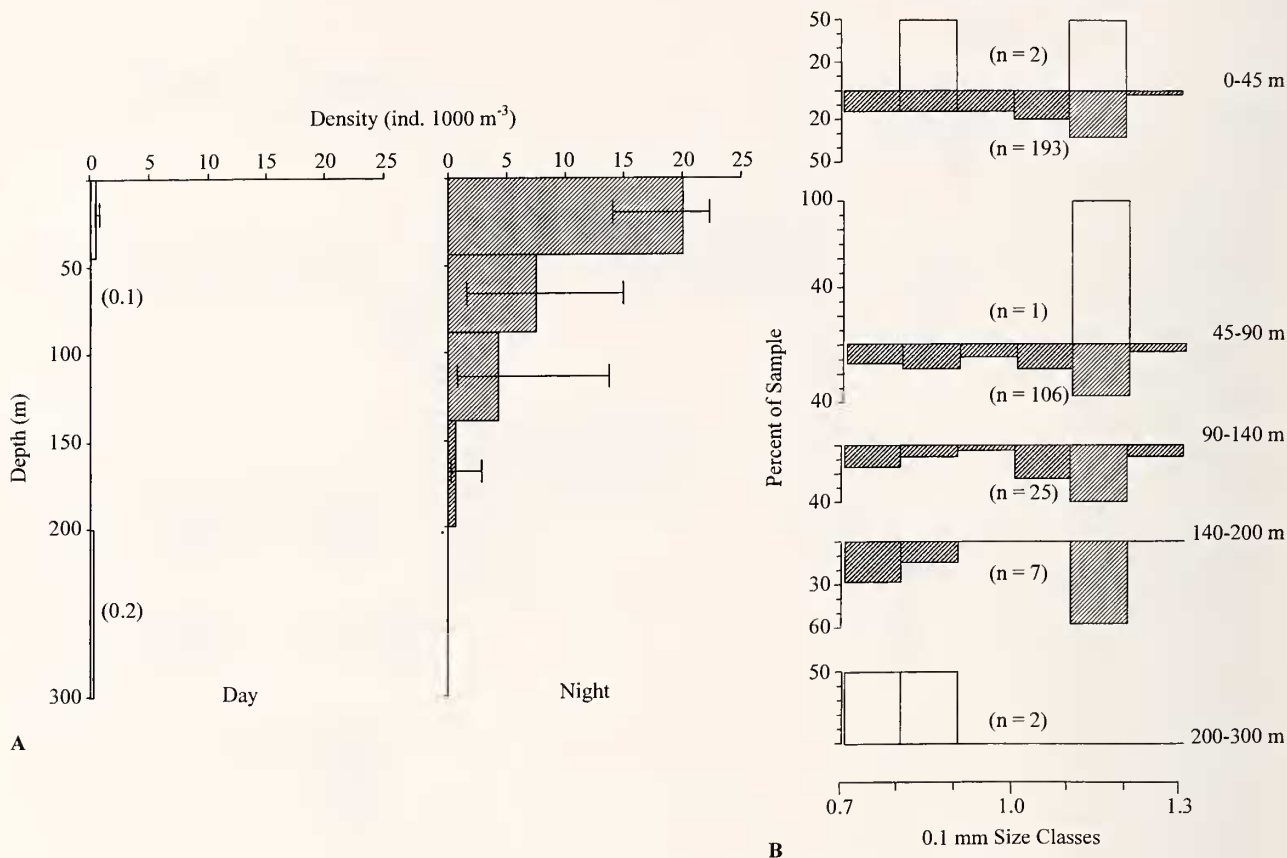
Figure 16. *Limacina lesueuri*. Legend as for Figure 4.

trochiformis was in the upper 140 m and no individuals of *C. virgula conica* were found below 140 m during either diel period. Downward nocturnal migration from the surface by adults of *C. virgula conica* in the Caribbean were reported by Haagensen (1976). There may be some evidence of this pattern in the present study, as nighttime densities were somewhat lower than daytime densities above 90 m.

The vertical distribution of "*Cavolinia longirostris*" was reported by Wormelle (1962). She found evidence of migrations in the Florida Current with 50% of the individuals above 219 m during the day and above 76 m at night. In contrast, Chen and Bé (1964) found no diel differences in surface waters (0–10 m) in the western North Atlantic. Comparison of these results with the present is not possible because "*C. long-irostris*" was split into 24 species by van der Spoel et al. (1993). One of these species, *Diacavolinia angulosa*, was identified in the present study. Which species (or multiple species) was represented by "*C. longirostris*" in Wormelle's study is not known.

Our results for *Diacria danae* and *D. costata* can be compared indirectly with three reports for *D. quad-ridentata* (de Blainville, 1821), which may actually represent one or both of the above species (discussed in Nigro, 2002). Off Hawaii, *D. danae* showed a pattern that was nearly identical to *D. costata,* remaining exclusively in the upper 140 m during both diel periods. There was some evidence of migration by individuals dwelling deeper than 90 m during the day to waters above 90 m at night, which is in general agreement with patterns found in the Caribbean by Haagensen (1976) and in the western North Atlantic by Wormelle (1962). However, in the surface waters of the western North Atlantic, Chen and Bé (1964) found no evidence of migration for *D. quadridentata.*

Ten of the 13 species assigned to the epipelagic/mesopelagic and mesopelagic species group appeared to undergo nocturnal vertical migrations in the present study; three Limacinidae (*Limacina inflata, L. buli-moides,* and *L. lesueuri*), and seven Cavoliniidae (*Styliola subula, Creseis acicula, Clio pyramidata, Cavolinia globulosa, Cavolinia inflexa, Cuvierina colum-nella,* and *Hyalocylis striata*). These species were either absent or present in low numbers in the upper 300 m during the day and in moderate to high numbers in the upper 140 m at night.

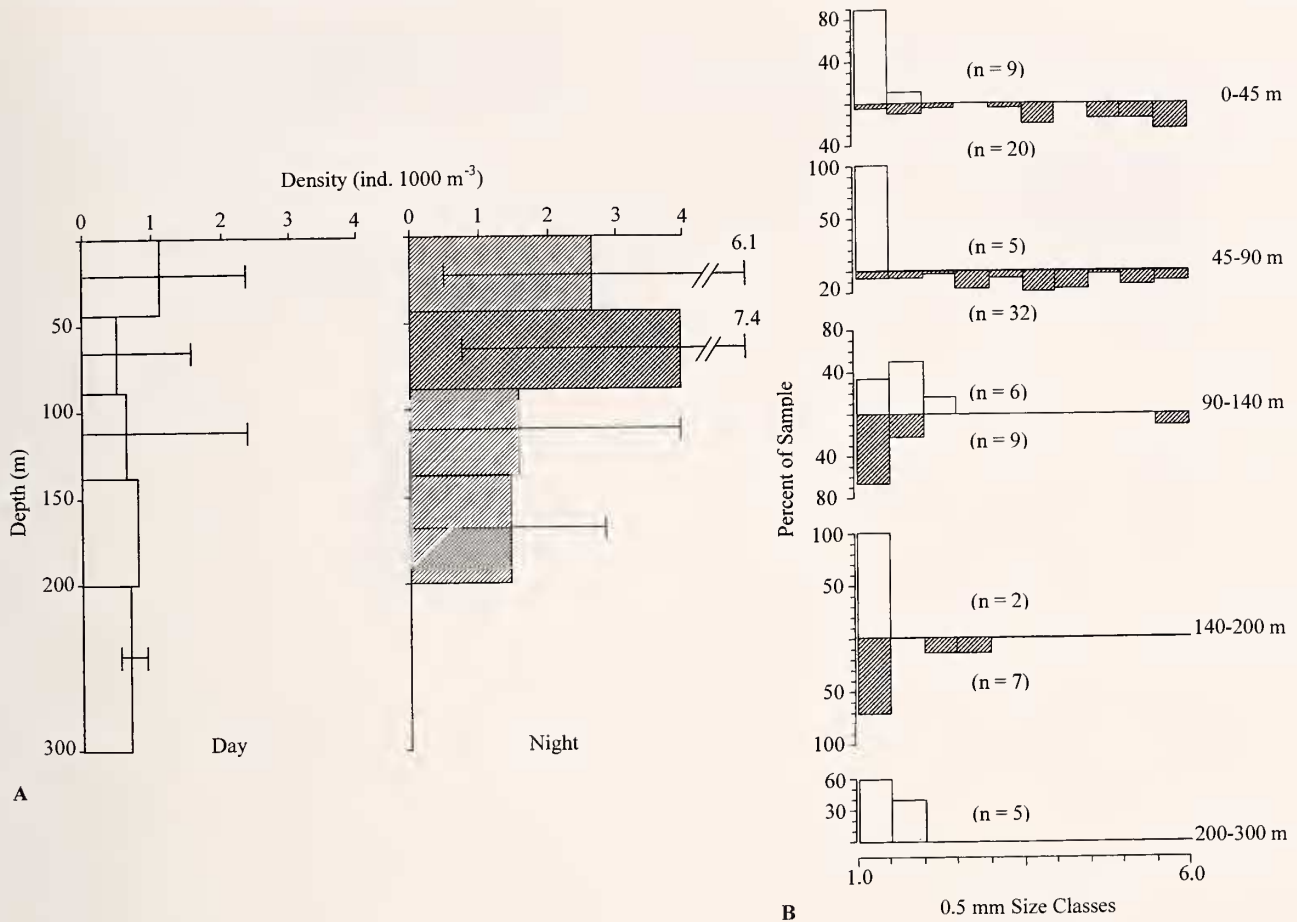Wormuth (1981) recorded *L. inflata* down to

Figure 17. *Cavolinia inflexa.* Legend as for Figure 4.

≥1000 m in the Sargasso Sea during the day with peak densities between 100 and 400 m. He found most of the individuals at night in the upper 75 m with a gradual decrease in numbers down to 125 m. In the present study, the total daytime density in the upper 300 m was 3.2% of the nighttime density. Assuming that night tows are a reasonable estimate of population density and that daytime net avoidance is either absent or not significant, then only 3.2% of the population occurred above 300 m during the day whereas >50% were found at depths above 100 m at night. These data correspond generally with the results described above from Wormuth from the Sargasso Sea. In marked contrast, Wormelle (1962) reported that in the Florida Current 50% of the individuals were captured above 236 m during the day and 232 m at night (i.e., no evidence of nocturnal migration).

Styliola subula and *Limacina bulimoides* were found by Wormuth (1981) to be vertical migrators in the Sargasso Sea, with most of each species population above 100 m at night and above 260 m during the day. In the present study, the water column density of *S.*

subula was 13 times greater at night than during the day (Table 1). Also, most of the specimens from the day samples were 1–3 mm, while those from the night tows ranged from 1–9 mm (Figure 13). These density and size differences suggest nocturnal migration of *S. subula* greater than 3 mm from depths below 300 m. For *L. bulimoides*, there were no diel differences in shell sizes, although in agreement with Wormuth there was an evident nocturnal vertical migration from waters below 140 m during the day to above 140 m at night. Wormuth (1986) reported that shell size increased with decreasing depth in the upper 100 m; most individuals ranged in size from 0.5 to 0.8 mm between 50 and 100 m, 1.2 to 1.4 mm between 25 to 50 m, and 1.3 to 1.5 mm from 0 to 25 m. Comparison of shell sizes in the 0–45 and 45–90 m intervals in our study, however, show no such vertical difference, especially at night where the size-frequency distributions were based on large sample sizes (Figure 14).

Myers (1967) reported maximum concentrations of *Creseis acicula* at night in the upper 50 m off Cape Hatteras, and Wormuth (1981) suggested that some
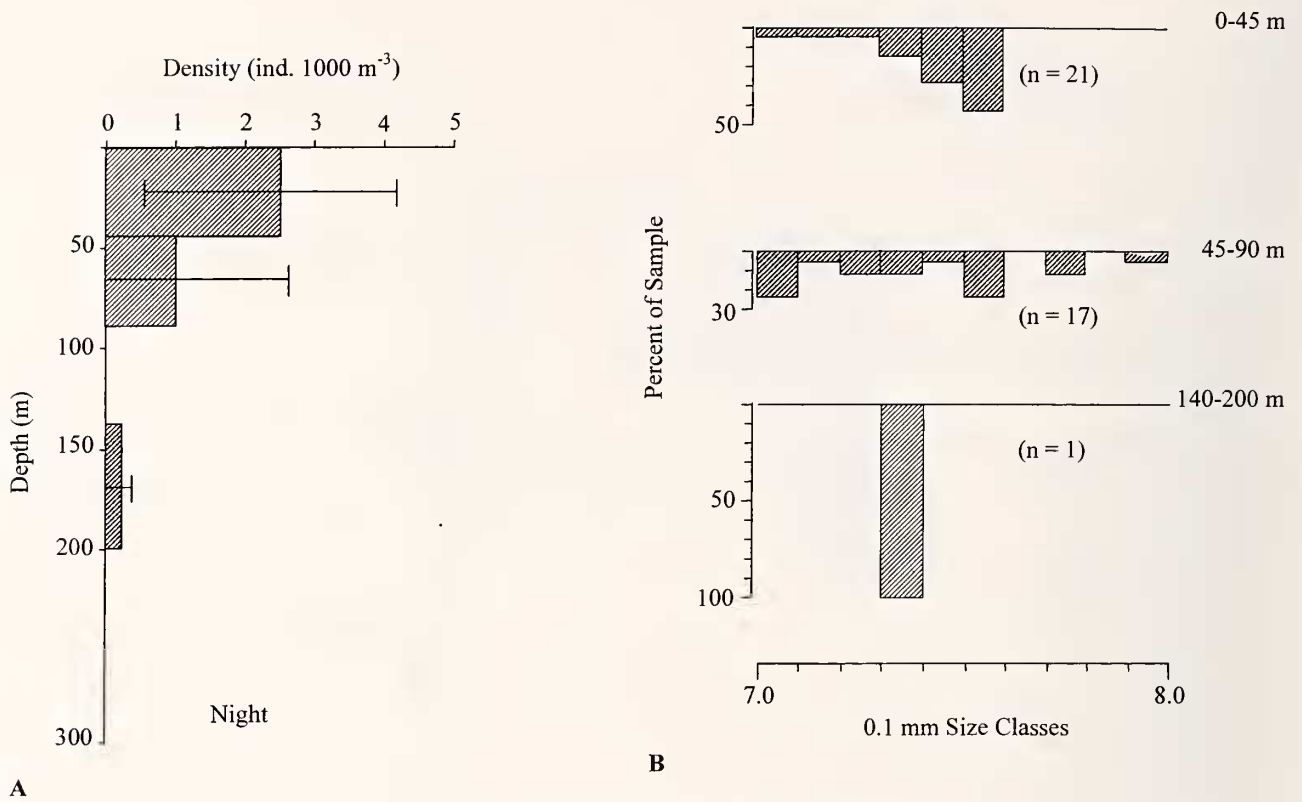
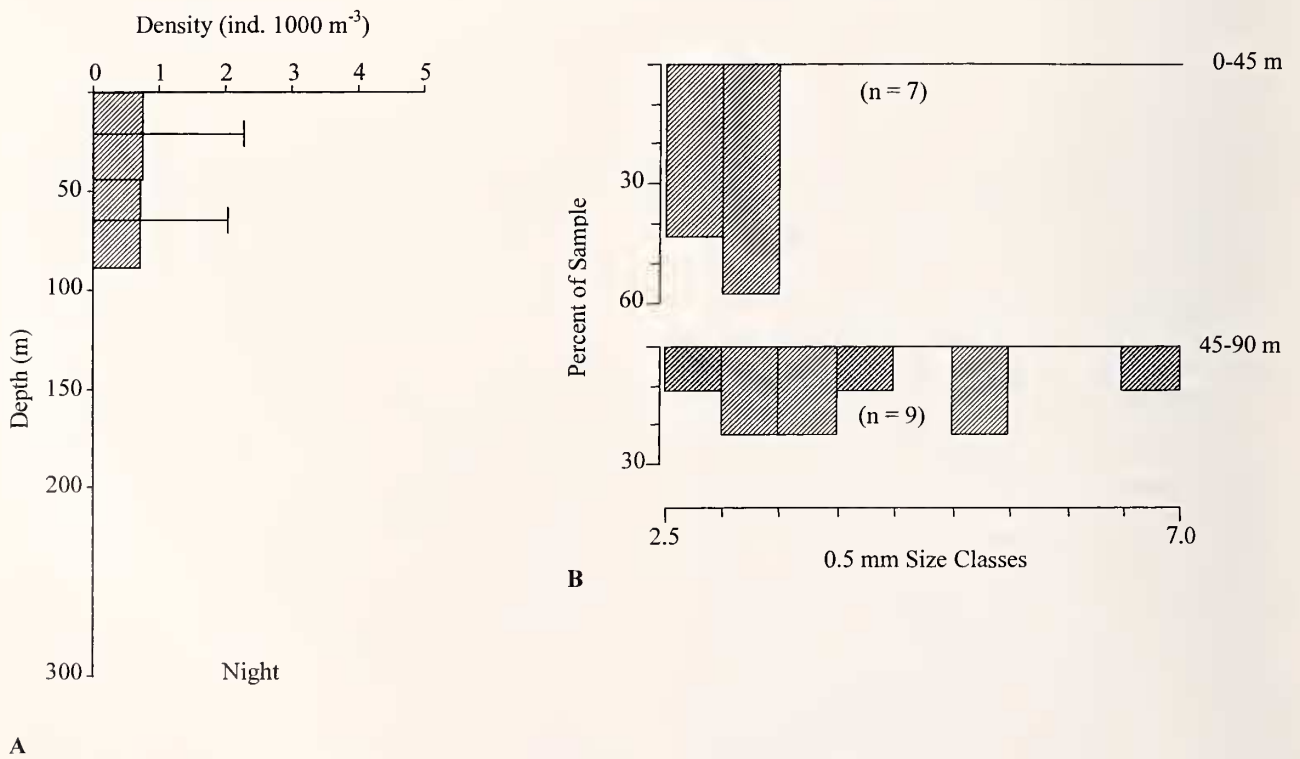Figure 18.   *Cuvierina columnella.* Legend as for Figure 4.

Figure 19.   *Hyalocylis striata.* Legend as for Figure 4.

Table 2

Geographic distribution of euthecosomes and comparison of species collected from the North and Equatorial Pacific Ocean by McGowan (1960) and the present study (indicated by asterisks). Only distinct species are listed; for those with known morphological variants (i.e., subspecies, varieties, or formae), the distribution includes all subspecific taxa. Species in bold print have tropical and/or subtropical distributions in the North Pacific Ocean. Sources of data are: 1) Bé and Gilmer (1977), 2) van der Spoel et al. (1993), 3) van der Spoel et al., (1997), 4) Bontes and van der Spoel (1998), and 5) van der Spoel and Dadon (1999). + = present, − = absent.

Species	Biogeographic Region				Source of Data	Mc Gowan (1960)
	Polar	Subpolar	Subtropical	Tropical		
Family Limacinidae						
Limacina bulimoides *	−	−	+	+	3,5	+
Limacina helicina	+	+	−	−	1	+
Limacina helicoides	−	−	+	+	5	−
Limacina inflata *	−	−	+	+	1,3,5	+
Limacina lesueuri *	−	−	+	−	1	+
Limacina retroversa	−	+	−	−	1,5	−
Limacina trochiformis *	−	−	+	+	3,5	+
Family Cavoliniidae						
Cavolinia gibbosa *	−	−	+	−	1	+
Cavolinia globulosa *	−	−	+	+	1	+
Cavolinia inflexa *	−	−	+	+	1	+
Cavolinia tridentata	−	−	+	+	1,5	+
Cavolinia uncinata	−	−	−	+	1	+
Clio andrae	−	−	+	+	5	−
Clio antarctica	−	+	−	−	1	−
Clio balantium	−	−	+	+	1	+
Clio campylura	−	−	−	+	3	+
Clio chaptalii	−	−	+	+	1,5	+
Clio convexa	−	−	−	+	1	−
Clio cuspidata	−	−	+	+	1,5	+
Clio polita	−	+	+	+	1	+
Clio pyramidata *	−	−	+	−	1	+
Clio recurva	−	−	+	+	5	−
Clio scheelei	−	−	+	−	3	−
Clio sulcata	−	+	−	−	1,5	−
Creseis acicula *	−	−	+	+	1,3,5	+
Creseis chierchiae	−	−	+	+	3,5	+
Creseis sp. *	−	−	+	−		−
Creseis virgula	−	−	+	+	1,3,5	+
Cuvierina columnella *	−	−	+	+	1	+
Diacavolinia angulosa *	−	−	−	+	2	+
Diacavolinia elegans	−	−	+	+	2	−
Diacavolinia longirostris	−	−	−	+	2	−
Diacavolinia mcgowani	−	−	−	+	2	−
Diacavolinia pacifica	−	−	+	+	2	−
Diacavolinia triangulata	−	−	−	+	2	−
Diacavolinia vanutrechti	−	−	+	+	2	−
Diacria costata *	−	−	−	+	3	−
Diacria danae *	−	−	+	+	3	−
Diacria maculata *	−	−	+	+	4	−
Diacria major *	−	−	+	+	4,5	−
Diacria quadridentata	−	−	−	+	3	+
Diacria rampali	−	−	+	+	4,5	−
Diacria schmidti	−	−	−	+	3	−
Diacria trispinosa	−	−	+	+	3,4,5	+
Hyalocylis striata *	−	−	+	+	1,3,5	+
Styliola subula *	−	−	+	+	1,3,5	+

shallow water migration by this species might take place to waters above 25 m at night in the Sargasso Sea. These findings agree with our results; at night more than 95% of the individuals were in the upper 90 m and 70% were in the upper 45 m. In both of the preceding studies, the daytime distribution was concentrated in the upper 100 m, while we found low daytime densities between the surface and 300 m.

Wormuth (1981) recorded *Clio pyramidata* down to 1000 m with peak abundances between 240 and 460 m during the day and in the upper 100 m at night. We found that only 4% of the individuals captured at night between the surface and 300 m were present in this depth range during the day, which is consistent with Wormuth's findings from the Sargasso Sea. The results of the two studies differ in that most of the nighttime population in the present study was between 100 and 200 m instead of the upper 100 m as Wormuth reported. The presence of small (1.0–1.1 mm) individuals during the day between 140 and 300 m, a broad size range (to 13.0 mm) at night, and those greater than 6 mm only collected in the upper 90 m at night strongly suggests nocturnal vertical migrations by the adult members of this species.

Limacina lesueuri was reported by Wormuth (1981) to be a nocturnal migrator with 50% of the individuals above 300 m during the day and above 100 m at night. Likewise, Haagensen (1976) reported more than 90% of the individuals above 274 m during the day and above 63 m at night. We found that the total daytime density was only 2% of the total nighttime density above 300 m, implying that most individuals in the population were deeper than the nets fished. At night, >50% of the individuals were in the upper 45 m. Thus, the daytime vertical range off Hawaii may be deeper than in the Sargasso Sea and the Caribbean; however, the nighttime depths of greatest abundance are similar.

Cavolinia inflexa was found by Haagensen (1976) to be a vertical migrator in the Caribbean, with 50% of the population sampled above 261 m during the day and 50% above 50 m at night. Similar results were obtained in this study, as the daytime density above 300 m was 40% of the night density. At night, >50% of the population sampled were found above 90 m.

In the Caribbean, Haagensen (1976) reported migrations of *Cuvierina columnella* from a depth range of 224 to 344 m during the day to above 65 m at night. Similarly, he found 50% of *Hyalocylis striata* above 243 m during the day and above 81 m at night. Wormelle (1962) reported similar findings for *H. striata* in the Florida Current with 50% above 283 m during the day and 84 m at night. In the present study, both species were absent from daytime tows and were limited to the upper 90 m at night, except for one *C. columnella* captured in the 150–200 m interval. During the day, the Bongo nets may have simply missed

individuals that were there or the nets did not fish deep enough to reach the minimum daytime depth of this species. Like the present study, Myers (1967) reported *C. columnella* and *H. striata* off Cape Hatteras to be absent during the day from tows above 150 m, but found both species to be concentrated in the upper 50 m at night.

Three (*Diacria maculata*, *Cavolinia gibbosa*, and *Diacria major*) of the 19 species of euthecosomes identified from Hawaiian waters were captured only at night in extremely low numbers, and comparisons with other studies are not warranted.

CONCLUSIONS

The diel distributions of the 16 most abundant species discussed above are in general agreement with the results obtained for the same species that occur in the North Atlantic Ocean and Caribbean Sea. Six of the species sampled here were permanent residents of the epipelagic zone and showed limited to no diel differences. The majority (10) were either absent or present in low numbers in the upper 300 m during the day and in higher numbers in the upper 140 m at night. If these low densities, or absence during the day, are a result of most of the species' populations residing below 300 m, then these ten species generally dwell in deeper waters off Hawaii than in the North Atlantic and Caribbean.

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